Flight Responses of Three Congeneric Species of Intertidal Gastropods (Prosobranchia : Neritidae) to Sympatric Predatory Gastropods from Barbados

BY

DANIEL L. HOFFMAN, WILLIAM C. HOMAN, JAY SWANSON AND PAUL J. WELDON [1]

Department of Biology, Bucknell University, Lewisburg, PA 17837

INTRODUCTION

LEWIS (1960) RECORDS AT LEAST 3 species of gastropods belonging to the genus *Nerita* inhabiting the mid to high rocky intertidal shores of Barbados; the Bleeding Tooth Nerite, *Nerita peloronta* (Linnaeus, 1758), the Variegated Nerite, *Nerita versicolor* (Gmelin, 1791), and the Checkered Nerite, *Nerita tessellata* (Gmelin, 1791). These grazing gastropods are broadly distributed throughout the Caribbean province from southern Florida and the Bahamas to as far south as Para, Brazil (RUSSELL, 1941). The 3 species show a well defined zonation with only a little overlap (HUGHES, 1971). Highest on the shore is *N. peloronta,* usually found on the surface of large seaward facing boulders above mean high water spring (MHWS) in exposed situations where they receive the full force of the surf; however, they are seldom submerged. *Nerita versicolor* generally is found at the same levels, but extending slightly below MHWS; it is most often limited to more protected areas. Lowest on the shore is *N. tessellata,* often, but not always, found submerged in small rocky tidal pools from mean low water (MLW) to the mean tide level (MTL). Hughes noted that *N. tessellata* has a mean density throughout the zone of 93.2 ± 20.8 SE/m^2 with the density increasing from the seaward to the landward edges; also that it generally prefers open shaded areas or the undersides of flat rocks.

There is a paucity of information concerning the behavior and ecology of these species. STEPHENSON & STEPHENSON (1950) described their zonation in the Florida Keys. LEWIS (1960) provided a description of zonation patterns and some aspects of their reproductive biology in Barbados. He also gave evidence for evaporative cooling in *Nerita tessellata* (LEWIS, 1963). KOLPINSKI (1964) studied the growth and life histories of these 3 species in Florida. In addition, population energy budgets were compiled for the 3 species of *Nerita* found on Barbados (HUGHES, 1971).

Presently there is relatively little known concerning possible predator-prey relationships between the species of *Nerita* and sympatric species of carnivorous gastropods. In fact, there have been no reports of predator-induced escape or avoidance behavior in the nerites in general, although representative species of most other families of archaeogastropods have been studied extensively (see ANSELL, 1969, for a general review).

During the month of January for 3 consecutive years from 1975 through 1977, we had the opportunity to make observations on predator-induced behavior of the 3 species of *Nerita* from Barbados both in the field and under laboratory conditions. We were especially interested in the effect of the high intertidal carnivorous thaidid gastropod, *Purpura patula* (Linnaeus, 1785) on the behavior of the nerites. This carnivore has been implicated by LEWIS (1960) as a predator of the chiton, *Acanthopleura granulata* (Gmelin. 1791) and the barnacle, *Tetraclita squamosa* (Bruguière, 1789), and overlaps the distribution of the 3 species of nerites in the rocky intertidal, from mean sea level (MSL) to a few feet above MHWS (LEWIS, *op. cit.*).

FIELD OBSERVATIONS

Observations on gastropods were made at 2 small indentures on the NE exposed rocky coast of Barbados, River Bay (13°19′N; 59°36′W) and Little Bay (13°18′N; 59° 35′W). Initially observations were made on *Nerita tessellata* that were found clustered in small (0.1 to 0.5 m diameter) tidal pools at low tide. Small pools that contained approximately 10 - 15 nerites were chosen for such observations. Specimens of predatory species of gastropods

[1] Present address: Department of Zoology, University of Tennessee, Knoxville, TN 37916

Table 1

The ability of different species of gastropods to elicit an escape response in the Checkered Nerite. *Nerita tessellata* Gmelin, in the field

Species[1]	Response[2]	Species[1]	Response[2]
Thais haemastoma floridana (Conrad, 1893)	XXX	*Bursa thomae* (Orbigny, 1842)	X
Thais rustica (Lamarck, 1822)	XXX	*Bursa granularis cubaniana* (Orbigny, 1842)	X
Thais deltoidea (Lamarck, 1822)	X	*Coralliophila caribaea* (Abbott, 1958)	X
Purpura patula (Linnaeus, 1758)	XXX	*Conus mus* (Hwass, 1792)	X
Leucozonia nassa (Gmelin, 1791)	XX	*Charonia variegata* (Lamarck, 1816)	X
Leucozonia ocellata (Gmelin, 1791)	XX	*Cittarium pica* (Linnaeus, 1758)	X

[1]At least five replicate observations were taken using different specimens of each species of snail. The addition of a nerite to an adjacent pool of snails served as control.

[2]X: response similar to control, little or no movement by the nerites; XX: activity evident, a few to many of the nerites crawled out of the pool by 15-20 minutes; XXX: full response, most of the nerites crawled out of the pool within 20 minutes.

were introduced to the center of the pool. Table 1 qualitatively records the ability of various intertidal and subtidal gastropods to elicit an avoidance or escape response in *N. tessellata.* The strongest response, *i.e.*, the nerites actually leaving the tidal pool in an arbitrarily determined time of 20 minutes, was most apparent in the presence of 3 species of thaidid gastropods, *Purpura patula, Thais haemastoma floridana* (Conrad, 1893), and *Th. rustica* (Lamarck, 1822); also to a lesser extent by the fasciolariids, *Leucozonia ocellata* (Gmelin, 1791) and *Leucozonia nassa* (Gmelin, 1791). No response was elicited by herbivorous forms or by gastropods that are subtidal by nature. The behavioral response of *N. tessellata* to the presence of carnivorous gastropods was elicited not by contact but by distance chemoreception. Initially the nerites elevated the anterior end of the shell exposing the head. The long pigmented cephalic tentacles began to flail back and forth in a violent manner; and then the snails exhibited increased locomotory activity which often, but not always, resulted in their leaving the pool of water. Many of the "escaped" nerites were so highly activated that they often moved a distance of 10 to 30 cm from the edge of the pool before coming to rest. The bottom of some small tidal pools held a few millimeters of fine sand, and on rare occasions the presence of a thaidid snail elicited a burrowing response by the nerite into the sand. In no case were any nerites captured or eaten during the course of our observations. However, *Purpura patula* was observed feeding during low tide on 13 separate occasions on *Nerita tessellata.* In all cases the carnivores were small specimens, averaging about 2.4 cm in length. The nerites had been overturned and the predator was covering the ventral surface with its large foot. Larger specimens (average size, 4.0 cm) were observed feeding on the chiton, *Acanthochiton granulata* (Hoffman & Weldon, 1978).

The responses of *Nerita versicolor* and *N. peloronta* to predatory gastropods were difficult to observe in the field at low tide because of their high and dry intertidal position. The open exposed situation of the rocky beach precluded any observations at high tide; therefore any behavioral information had to be collected under laboratory conditions.

EXPERIMENTAL METHODS

The following experiment was designed to test whether the 3 species of *Nerita* in question would demonstrate an escape response to the thaidid gastropod, *Purpura patula,* in the laboratory; and to determine whether such behavior, if evident, was induced by contact or distance chemoreception. Six specimens of either *Nerita tessellata, N. versicolor,* or *N. peloronta* were placed into glass fingerbowls (top diameter, 11.5 cm) each of which contained approximately 150 mL of sea water. The *N. tessellata* ranged in shell length from 1.2 to 1.9 cm; the *N. versicolor*, 1.0 to 2.0 cm; and the *N. peloronta*, 1.4 to 3.3 cm. The *Purpura patula* tested had an average shell length of 2.6 cm. The experiments were designed to collect both descriptive and quantitative data by counting the number of nerites leaving the water in an arbitrarily determined time of 30 minutes after adding the predator or an aliquot of sea water that contained the predator's "scent". In order to standardize the procedures the following steps were taken:

1) After being placed in the bowls the snails were allowed to come to rest, usually 15 - 20 minutes before adding the predatory snail; 2) the experiments were performed between 0800 and 1100 Barbados time under the subdued lighting conditions of the laboratory; 3) an additional nerite was added to each of the control bowls in order to mimic the presence of the predator; 4) to test for distance chemoreception, approximately 25 mL of water taken from a container that held one *P. patula* per 100 mL of sea water was carefully added to the fingerbowl that contained nerites. The control for this experiment entailed adding approximately 25 mL of sea water from the intake sea water valve to a bowl of nerites. All data were tested for significance using the Chi-square Test for 2 independent samples (SIEGEL, 1956).

EXPERIMENTAL RESULTS

Statistically significant data were obtained demonstrating that the presence of *Purpura patula* would elicit an escape response in all 3 species of nerites tested (Table 2). Locomotory activity was exhibited in both experimental and control bowls; this was most apparent with both *Nerita versicolor* and *N. peloronta*. As high intertidal forms, the act of being submerged stimulates them to activity, so it was not surprising to observe such activity under experimental conditions. All 3 species displayed tentacular flailing in the presence of *P. patula*, a phenomenon that was not evident under control conditions. Since the specimens of *P. patula* that were used in these experiments did not move, but remained attached to the center of the bowls, it appeared that contact was not necessary to trigger the response in any of the species.

The ability to react positively to the "scent" of *Purpura patula* was demonstrated most strongly by *Nerita tessellata* in the water experiments. Although all 3 species of nerites demonstrated some capacity to react to this "scent water", *e.g.*, heightened cephalic tentacular flailing, only *N. tessellata* data were statistically significant at the 0.05 level and beyond (Table 2). The lack of significance in the response of *N. versicolor* and *N. peloronta* may be a function of small sample size. Also, since these last 2 species would never encounter the still water conditions of the tidal pool, but only the surges of the tide, their responsiveness to a predator may be impaired or diminished under such experimental conditions.

Nerita versicolor alone demonstrated a strong negative response to light in that all the snails that emerged from the water in the bowls would do so on the side opposite the incident light. If the bowls were rotated 180°, positioning the active snails immediately before the light, the directional movement would be abruptly changed by 180°; in fact, the nerites often crawled back into the water and exited from the opposite side of the bowl.

Table 2

Summary of the ability of *Purpura patula* or water containing the "scent" of *Purpura patula* to elicit an escape response in three species of *Nerita* from glass fingerbowls

	No. of nerites in expt. bowls at T_0	No. to leave bowls at T_{30}	No. of nerites in control bowls at T_0	No. to leave bowls at T_{30}	Chi-square
Purpura patula					
Nerita tessellata	144	126	126	64	41.75[3]
Nerita versicolor	72	72	84	73	8.27[3]
Nerita peloronta	54	50	42	32	3.86[3]
Purpura patula water					
Nerita tessellata	84	59	72	18	29.88[3]
Nerita versicolor	72	70	72	63	3.53[3]
Nerita peloronta	42	41	42	36	2.49[3]

[3]The difference between the experimental and control group is significant ($p \leq 0.05$) when the Chi-square is greater than 3.840.

DISCUSSION

The 3 species of Barbadian nerites exhibit escape of flight behavior that is similar to many trochid gastropods (CLARK, 1958; FEDER, 1963; YARNALL, 1964; HOFFMAN & WELDON, 1978). There was no qualitative difference in the behavioral response of the 3 congeners to *Purpura patula*. The fact that no shell twisting or rotating was shown by any of the nerites gives strength to the argument raised by Hoffman & Weldon that such behavior may serve as an additional adaptation to contact-induced flight behavior as is the case in the top shell, *Tegula excavata* (Lamarck, 1822).

It appears that submergence and light, and perhaps even moving water, may play significant roles in either stimulating or increasing the locomotory behavior of high intertidal forms like *Nerita versicolor* and *N. peloronta*, and should not be overlooked in studies dealing with predator-prey interactions. *Nerita versicolor* may be similar to the Kenyan nerite, *Nerita plicata* (Linnaeus, 1758), which orients itself in the intertidal by alternating positive and negative phototaxes during the morning and afternoon hours of the day (WARBURTON, 1973). Certainly further observations are necessary before we can determine what cues these high intertidal snails use to avoid predation and maintain their position on the beach.

The relatively strong response of *Nerita tessellata* to *Purpura patula*, as well as to other sympatric thaidid and fasciolariid gastropods has ramifications in the predator-prey interactions of these species. The fact that *P. patula* can be observed feeding on *N. tessellata* in the field gives credence to this argument. However, more ecological data are needed before any definitive role of the nerites in the diet of these carnivores can be assigned.

ACKNOWLEDGMENTS

We wish to thank Dr. Finn Sander, the Director of the Bellairs Research Institute of McGill University for facilities and warm hospitality afforded us while in Barbados. Also to Dr. Joseph Rosewater, Division of Malacology, the U. S. National Museum for identifying certain species of gastropods. And finally to Marcy Gelman, Craig Franz, Joe McGinley, Jeff Churchill, and Debbie Barnard for their much appreciated assistance in the field.

Literature Cited

CLARK, W. C.
1958. Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. Nature 181 (4602): 137 - 138

FEDER, HOWARD MITCHELL
1963. Gastropod defense responses and their effectiveness in reducing predation by starfishes. Ecology 44 (3): 505 - 512

HOFFMAN, DANIEL L. & PAUL J. WELDON
1978. Flight responses of two species of intertidal gastropods (Prosobranchia: Trochidae) to sympatric predatory gastropods from Barbados. The Veliger 20 (4): 361 - 366 (1 April 1978)

HUGHES, R. N.
1971. Ecological energetics of *Nerita* (Archaeogastropoda, Neritacea) populations on Barbados, West Indies. Marine Biol. 11: 12 - 22

KOLPINSKI, M. C.
1964. The life history, growth and ecology of four intertidal gastropods (genus *Nerita*) of southeast Florida. Unpubl. Ph. D. dissertation, Univ. Miami

LEWIS, JOHN B.
1960. The fauna of rocky shores of Barbados, West Indies. Canad. Journ. Zool. 38: 391 - 435; 20 figs.
1963. Environmental and tissue temperatures of some tropical intertidal animals. Biol. Bull. 124: 277 - 284

RUSSELL, D. M.
1941. The recent mollusks of the family Neritidae of the western Atlantic. Bull. Mus. Comp. Zool. Harvard 88: 347 - 404

SIEGEL, SIDNEY F.
1956. Nonparametric statistics for the behavioral sciences. 312 pp., McGraw-Hill, New York

STEPHENSON, T. A. & ANNE STEPHENSON
1950. Life between tide marks in North America. 1. The Florida Keys. Journ. Ecol. 38: 354 - 402

WARBURTON, K.
1973. Solar orientation in the snail *Nerita plicata* (Prosobranchia, Neritacea) on a beach near Watamu, Kenya. Marine Biol. 23: 93 - 100

YARNALL, JOHN L.
1964. The responses of *Tegula funebralis* to starfishes and predatory snails (Mollusca: Gastropoda). The Veliger 6 (Supplement): 56 to 58; 2 tables (15 November 1964)